

INHERITANCE OF DELAYED FLOWERING IN
SOYBEANS (Glycine max (L.) Merrill)

BY

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1988

2

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J. Emmanuel Bidja Mankono

This dissertation is dedicated to
my father, Basil A. Mankono Bidja
my wife, Rachel Bidja
and my daughter, Armelle M. Mfegue
who have always given me their best in love,
friendship, understanding, and counsel.

ACKNOWLEDGMENTS

I express my sincere gratitude to my major professor, Dr. Kuell Hinson. His assistance, counsel, guidance, and moral support during the course of these studies and in the preparation of the manuscript are greatly appreciated.

My gratitude is extended to Dr. Paul Pfahler, Dr. Wayne Sherman, Dr. Rex L. Smith, Dr. David D. Baltensperger, and Dr. Kenneth Buhr for their constructive criticism and suggestions during the review of this dissertation.

I am grateful to Mr. Frank McGraw for his assistance and cooperation during the conduct of the field experiment.

Finally, I thank all the Cameroonian students who helped me in the field work.

TABLE OF CONTENTS

	PAGE
ACKNOWLEDGMENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES.....	ix
ABSTRACT.....	x
INTRODUCTION.....	1
LITERATURE REVIEW.....	5
MATERIALS AND METHODS.....	10
Sources of Plant Materials.....	10
Crosses and Segregating Populations.....	13
RESULTS AND DISCUSSION.....	22
Crosses Among Late Flowering Lines.....	22
1986 F ₂ Populations.....	22
1987 F ₃ Data.....	38
F ₂ Populations of 1986 Crosses.....	43
1986 Progeny Tests of Late-generation Rows.....	57
1987 Progeny Tests of Late-generation Rows.....	63
SUMMARY AND CONCLUSIONS.....	68
APPENDIX.....	70
REFERENCES.....	88
BIOGRAPHICAL SKETCH.....	93

LIST OF TABLES

TABLE		PAGE
1	Parentage of isolines and segregating rows used in this study.....	11
2	Year crosses were made and when F ₁ and F ₂ were grown.....	14
3	Source of late-generation parent rows exhibiting apparent segregation for flowering date in 1985.....	18
4	Parent rows whose progenies were tested in 1987.....	19
5	Parental and hybrid parameters of crosses between late flowering lines.....	24
6	Means of parents, midparents, F ₁ , and F ₂ for flowering response for the 1986 season.....	25
7	Observed numbers for early and late flowering classes in each F ₂ population of Will X F85-1138 cross and chi-square and homogeneity values.....	30
8	Observed numbers for early and late flowering classes in each F ₂ population of Will X F85-1226 (grown in 1986) and L63-3117 X F85-1226 crosses and chi-square and homogeneity values.....	33
9	Analysis of F ₂ plant genotypes from three crosses inferred from F ₃ rows planted 15 June and 19 August 1987.....	40
10	Analysis of segregating F ₃ rows from F ₂ plants of four crosses planted 15 June and 19 August 1987.....	41
11	Means of parents, midparents, F ₁ , and F ₂ for flowering response for the 1987 season.....	45

TABLE	PAGE
12 Observed numbers for early and late flowering classes in F_2 population of F85-1226 X F85-1221 and F85-1136 X F85-1136 crosses and chi-square and homogeneity values.....	50
13 Observed numbers for early and late flowering classes in each F_2 population of Will X F85-1226 (grown in 1987) and Forrest X F85-1226 crosses and chi-square and homogeneity values.....	52
14 Observed numbers for early and late flowering classes in each F_2 population of F85-431 X PI 159925 and Bedford X PI 159925 crosses and chi-square and homogeneity values.....	56
15 Heritability estimates in percent.....	58
16 Segregation of parent rows 8209, 8361, and 8363 tested in 1986.....	60
17 Segregation of parent rows 8375, 8505, and 8566 tested in 1986.....	62
18 Segregation of parent rows 8210-7124, 8258-7239, 8258-7244, 8278-7271, and 8278-7277 tested in 1987.....	64
19 Segregation of parent rows 8304-7289 and 8460 progeny tested in 1987.....	66
20 Frequency distribution of parents, F_1 and F_2 progeny of crosses among delayed flowering genotypes.....	71
21 Frequency distribution of Will (P1), F85-1138 (P2), F_1 , and F_2 for flowering periods under three planting dates.....	73
22 Frequency distribution of L63-3117 (P1), F85-1138 (P2), F_1 , and F_2 for flowering periods under two planting dates.....	74
23 Frequency distribution of Will (P1), F85-1226 (P2), F_1 , and F_2 for flowering periods under three planting dates.....	75

TABLE	PAGE
24 Frequency distribution of L63-3117 (P ₁), F85-1226 (P ₂), F ₁ , and F ₂ for flowering periods under two planting dates.....	76
25 Frequency distribution of Bedford (P ₁), F85-1138 (P ₂), F ₁ , and F ₂ for flowering periods under three planting dates.....	77
26 Frequency distribution of Gordon (P ₁), F85-1138 (P ₂), F ₁ , and F ₂ for flowering periods under two planting dates.....	78
27 Frequency distribution of Bedford (P ₁), F85-1313 (P ₂), F ₁ , and F ₂ for flowering periods under three planting dates.....	79
28 Frequency distribution of Gordon (P ₁), F85-1313 (P ₂), F ₁ , and F ₂ for flowering periods under two planting dates.....	80
29 Frequency distribution of segregating F ₃ rows from Will X F85-1138 for flowering periods.....	81
30 Frequency distribution of segregating F ₃ rows from Will X F85-1226 for flowering periods.....	82
31 Frequency distribution of segregating F ₃ rows from Bedford X F85-1313 for flowering periods.....	83
32 Frequency distribution of parents and hybrids of two crosses between isoline pairs for flowering periods under two planting dates.....	84
33 Frequency distribution of Will X 1226/1221 for flowering periods under two planting dates.....	85
34 Frequency distribution of Bedford (P ₁), PI 159925 (P ₂), F ₁ , and F ₂ for flowering periods under two planting dates.....	86
35 Frequency distribution of late-generation rows 8304-7289 and 8460 for flowering periods under long-day conditions.....	87

LIST OF FIGURES

FIGURE		PAGE
1	Distribution of days to flower for F_2 populations from crosses between late flowering lines.....	23
2	Distribution of days to flower for F_2 populations from crosses having F85-1138 as one parent.....	29
3	Distribution of days to flower for F_2 populations from 1985 crosses having F85-1226 as one parent.....	32
4	Distribution of days to flower for F_2 populations from crosses, having F85-1138 as one parent, whose variation was continuous.	35
5	Distribution of days to flower for F_2 populations from crosses having F85-1313 as one parent.....	37
6	Distribution for days to flower for crosses among isoline pairs.....	48
7	Distribution of days to flower for F_2 populations from crosses between Will and Forrest and the isoline pair F85-1221/1226.....	51
8	Distribution of days to flower from F_2 populations from crosses having PI 159925 as one parent.....	54

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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August 1988

Chairman: Dr. Kuell Hinson
Major Departement: Agronomy

A character which delays flowering in soybeans (Glycine max (L.) Merrill) under short-day conditions has been identified in 'PI 159925'. The incorporation of that trait into varieties adapted to temperate regions may increase their range of adaptation to the tropics and subtropics. Isolines with and without the delayed flowering trait have been developed at Gainesville, Florida (29° 40' N). Because initial observations suggested that three gene pairs controlled the delayed flowering trait and later studies suggested one recessive gene, further studies of the inheritance of the delayed flowering trait were made.

The source of the delayed flowering trait was PI 159925. Four types of populations were studied in 1986 and 1987: a) five F₂ populations derived from intercrossing delayed-flowering genotypes, b) seventeen F₂ populations derived from crossing delayed flowering with conventional

genotypes, c) progenies of four selected F_2 populations, and d) progenies from F_8 or F_9 rows still segregating for variation in flowering date. These populations were planted at Gainesville, Florida, in early June, mid-July, and mid-August. Photoperiods (including twilight) at emergence were 15h, 14h 40min, and 13h 50min.

The F_2 populations from crosses among delayed flowering parents exhibited continuous variation that was not greater than that between the parents. Thus, parents do not have different major genes for delayed flowering.

The F_2 populations from 14 of 17 crosses produced discrete or near discrete classes. Chi-square tests gave good fits to a 3 early:1 late ratio. In progeny tests, F_3 rows formed 1:2:1 ratios. No early plants were produced in the progeny of F_2 plants classed as delayed flowering, thus discrediting a 13 early:3 late ratio in F_2 .

Progenies from late-generation rows gave good fit to a 3:1 ratio. However, two of the progenies were consistent with a 1 early:3 late ratio, indicating a dominant gene for late flowering. The possibility of two gene pairs affecting the delayed flowering trait derived from PI 159925 was discredited by F_3 data. This suggests a source other than PI 159925 for this dominant gene.

These results show that the delayed flowering trait from PI 159925 is controlled by two alleles at one locus with early flowering being nearly completely dominant.

INTRODUCTION

The soybean (Glycine max (L.) Merrill) is exploited for three major products: beans, oil, and meal. The oil is mainly used for human consumption and the meal as a high protein source for incorporation into animal and poultry feeds. More and more, soybean is being considered as an inexpensive source of high quality protein for human diets for the third world countries located in tropical and subtropical regions.

Due to breeding programs, the adaptation of soybean is very broad (45). However, according to Rachie and Plarre's 1979 publication (38), soybean production in the tropics had been mainly restricted to high-land regions. Soybean growing should be increasingly extended to low-land regions if high production is to be achieved. Introduction of improved lines is one the principal breeding methods used in many tropical countries. Many of these introductions are from temperate latitudes. Tropical latitudes differ from temperate latitudes manifesting short daylengths with little variation throughout the year. When varieties or lines adapted to temperate regions are planted in the tropics, they flower too early, thereby have less growth resulting in poor yields (13, 41). Hartwig (21) suggested a minimum of

45 days from emergence to flowering for adequate vegetative growth before first bloom. Rachie and Plarre (38) suggested using cultivars showing no response to short-day conditions in the tropics. However, the effectiveness of the photoperiod-insensitive trait is doubtful in the production field (25).

A character which caused delayed flowering in soybean under short-day conditions has been identified in 'PI 159925', a maturity group VIII line. Unlike other maturity group VIII lines which flower in approximately 30 days after emergence when grown under short-day conditions, PI 159925 flowers in about 50 days (23). The delayed flowering character can be backcrossed into temperate varieties or lines to produce varieties capable of adequate vegetative growth and good production under tropical conditions.

The incorporation of the delayed flowering trait in soybean varieties may also be beneficial to the USA. Board and Hall (8) reported that, in Louisiana, yield losses at nonoptimal planting dates caused by premature flowering induced by short-day conditions can be avoided by planting varieties with a long vegetative period.

The time of flowering in soybean is generally considered to be quantitatively inherited. However, three major genes affecting flowering time have been identified.

Bernard (5) reported that two independent gene pairs affect time of flowering and maturity in soybean. In

'Clark' (e_1E_2), the common genetic background used in the study, the gene E_1 , when substituted by backcrossing for e_1 , caused a 23- and 18-day delay in time of flowering and time of maturity, respectively, in central Illinois (40° N latitude). The gene e_2 , when substituted for E_2 , hastened flowering time and maturity time by 7 and 14 days, respectively.

Buzzell (11) reported that the dominant E_3 allele gave a sensitive response to long-fluorescent light that caused delayed flowering and late maturity. Its recessive e_3 allele gave an insensitive response and earlier maturity.

Hartwig and Kihl (24), using PI 159925 as one the parents with the delayed flowering trait, reported that as many as three genes were involved in the control of the delayed flowering character found in PI 159925.

PI 159925 is the source of the late flowering trait used and under investigation at Gainesville, Florida.

Azlan (4) suggested that delayed flowering resulted from a single recessive gene. However, in the F_2 populations he studied, flowering date classes often were not discrete. Nondiscrete classes were believed to be caused by segregation for quantitative genes affecting flowering date. But the possibility of a second major gene influencing flowering date was not excluded.

Malo (32) used highly inbred (F_8) selections from plant rows segregating for late flowering. In her study,

most progenies produced ratios of 3 early:1 late. This showed that a single recessive gene pair resulted in late flowering plants. However, three of Malo's twenty-six progenies appeared to segregate for more than one gene having a major effect on flowering date.

Furthermore, in the development of isolines with and without the delayed flowering trait, some late-generation rows appeared to contain more than two flowering-date classes. There was, therefore, a need for further studies to determine a) whether the genetic stocks investigated and used in the development of isoline pairs contain more than one major gene for flowering date and b) whether selected lines with the delayed flowering trait differ from standard varieties by one major gene or more than one major gene.

This dissertation reports the results from those studies.

LITERATURE REVIEW

In 1920, Garner and Allard (17) recognized the significance of daylength in determining the flowering behavior of soybeans and termed the response "photoperiodism." Later, it was shown that the length of darkness was the controlling factor (18). Soybeans have been classified as quantitative short-day plants, that is, they flower quickly when subjected to photoperiod shorter than a critical maximum (2, 9). However, a dark period was not a prerequisite for floral initiation in some cultivars (15). Such cultivars were mainly early maturing germplasm and were termed photoperiod insensitive or day neutral (15, 33, 37).

Photoperiodic response of a variety is a significant factor in determining its adaptation to a particular geographic area (14, 22, 46). A system of maturity group (MG) classification has been adopted for North America. Cultivars are placed in 13 groups from MG 000 to X. MG 000, 00, 0, and I are adapted to higher latitudes; higher numbered groups are adapted to lower latitudes (22, 46).

Temperature has been shown to affect the flowering behavior of soybeans. Roberts and Struckmeyer (39) reported that the flowering of two soybean cultivars ('Biloxi' and

'Chippewa') was inhibited by low temperatures. Increased temperatures were found to hasten flowering up to an optimum temperature of 28°C, above which flowering was delayed (42). Night temperatures are important in determining the photoperiodic response of soybeans (27, 36). Parker and Borthwick (35), found that with warm temperatures during the day, a 10°C night temperature limited the amount of flower initiation which occurred. Temperature effects on flowering time of soybeans are even more pronounced in tropically adapted cultivars. A 5°C change in day temperature was found to be more effective than 100 minutes change in daylength in influencing time of first flower (44). Temperature and daylength appear to interact in their control of the onset of blooming. Cooler temperatures and longer daylengths encountered at northern latitudes were reported as being additive in their delaying effects on flowering (31).

Delayed planting has been shown to affect both flowering and maturity dates in soybeans (7, 8, 14). When planted late, the post-flowering period was decreased for early cultivars, whereas the pre-flowering phase was shortened in late-maturing cultivars (1, 20).

In soybeans, flowering date has generally been considered to be quantitatively inherited. Byth (12) studied the cross between 'Manloxi' and 'Avoyelles'. The F_2 mean for days to flowering was consistently smaller than the

midparent value; thus, he concluded that dominance for early flowering was exhibited in the population he studied. Furthermore, he termed the inheritance of flowering time as being complex.

There are few reports of major genes affecting flowering date in soybean. Owen (34), studying the cross between 'Black Eyebrow' and 'J5', concluded that a major gene pair affected time of maturity (which he measured by time of flowering). He designated these two alleles at one locus E_e .

Two independent gene loci with two alleles at each locus affecting time of flowering and time of maturity have been described by Bernard (5). The effects of gene pairs E_1e_1 and E_2e_2 were analyzed in a common genetic background, 'Clark' (e_1E_2). The gene E_1 , when substituted by backcrossing for e_1 , caused a 23- and 18-day delay in flowering and maturity, respectively. The gene e_2 , when substituted for E_2 , resulted in 7 and 14 days earlier flowering and maturity, respectively. Lateness was found to be partially dominant at each locus. However, in combination, the two gene pairs are additive in effect.

Buzzell (11) reported that the dominant E_3 allele which gave a sensitive response to a long-fluorescent photoperiod caused delayed flowering and maturity, whereas the recessive e_3 allele gave an insensitive response and a resultant earlier flowering and maturity. In the field, e_3

appeared to affect flowering and maturity, hastening them about 7 days (6), when substituted in Clark for the normal E_3 . Kilen and Hartwig (30), studying the crosses 'Dorman' X 'Hill' and 'Arksoy' X 'Lee' (Hill and Lee are insensitive to light quality), concluded that the light-quality sensitive character acted as a monogenic recessive.

Kiihl (29), studying the cross between 'D72-7842' and 'Santa Maria', concluded that the late flowering character of Santa Maria, under short-day conditions, was controlled by recessive genes. Hartwig and Kiihl (24), using Santa Maria and PI 159925 as sources of delayed flowering trait, concluded that the late flowering character, under short-day conditions, was recessive and controlled by as many as three genes. However, later studies indicated that the delayed flowering character from PI 159925 was controlled by a single recessive gene (4, 32).

In order to reduce the problem of adaptation of temperate cultivars to tropical short-day conditions, particular effort has been devoted to the identification of day-neutral strains (15, 33, 37). However, it was shown that day neutral cultivars flower too early to be useful in the tropics. Hinson and Hartwig (26) suggested the use of strains with a long period from emergence to flowering to enhance the opportunities for adequate growth. Strains that flower in approximately 50 days under short-day conditions have been identified (21, 23, 24). PI 159925 was one of

those lines, thus, it is important to obtain information on the inheritance of its delayed flowering trait to better design breeding programs in the tropics.

MATERIALS AND METHODS

Sources of Plant Materials

Sources of parents with the gene for delayed flowering are shown in Table 1. These came from a program at Gainesville to develop a large number of near isolines, with and without the delayed flowering trait, in several maturity classes and with moderate diversity in genetic background. Development was as follows: crosses were made at Gainesville and F_1 plants were grown in Puerto Rico (winter nursery). The F_2 plants were grown at Gainesville. Early maturing F_2 plants were selected for growing F_3 plant rows in Puerto Rico. Early maturing plants were harvested from segregating rows and F_4 plant rows were grown at Gainesville. The process was repeated in F_5 , F_6 , F_7 , and F_8 with growing locations being alternated between Puerto Rico and Gainesville.

Each pair of F_8 lines were derived from two plants selected from the same F_7 row which in turn traced to one F_6 plant. In the F_6 generation the theoretical heterozygosity remaining is $3 \frac{1}{8}$ of that in the F_1 generation. Thus, lines developed are only near isolines. However, they are referred to as isolines throughout the text. For all

Table 1: Parentage of isolines and segregating rows used in this study.

Cross desig- nation	Parentage	1985 Generation
1	PI 417150A X [Kirby X (Forrest (3) X D77-12480*)]	F ₈
2	[Kirby X (Forrest (3) X D77-12480)] X Will	F ₈
3	[Kirby X (Forrest (3) X D77-12480)] X Forrest	F ₈
4A	Kirby X (Forrest (3) X D77-12480)	F ₈
4B	same	F ₉

*D77-12480 is a selection from Tracy X (Hill X PI 159925)

crosses, isolines were at the eighth generation except for cross 4 which had some isolines at the eighth generation and others at the ninth generation. These are designated cross 4A and cross 4B, respectively. Two isolines, F85-1221 and F85-1226, were selected in Puerto Rico whereas the others were selected at Gainesville. PI 159925, a plant introduction from Peru, is the original source of the delayed flowering trait. Hartwig and Edwards (23) evaluated PI 159925. They found that, unlike other maturity group VIII lines which flower in approximately 30 days after emergence when grown under short-day conditions, PI 159925 flowers in about 50 days. D77-12480, a selection from Tracy X (Hill X PI 159925), is the source of the delayed flowering character used in this study.

The crosses (Table 1) from which parent lines were selected were made to produce isolines with a wide range in flowering date. 'PI 417,150A', 'Will', 'Forrest', and 'Kirby' which contribute approximately 50% of the genes to crosses 1, 2, 3, and 4, respectively, are in maturity groups 0, III, V, and VIII, respectively. Maturity group III genotypes, adapted to Central Illinois, and earlier groups, begin flowering within 30 days after planting at Gainesville, almost regardless of planting date. By contrast adapted maturity group VII and VIII genotypes normally begin flowering between 48 and 60 days after a 1 June planting. Conventional type members of isoline pairs

selected range from about maturity group III through group VIII in flowering date, thus they flower in 30 to 60 days after a 1 June planting. Therefore in the conduct of this study, some delayed flowering parental genotypes (e.g. F85-1138) flowered earlier than many conventional type parents.

Crosses and Segregating Populations

'Bedford' (maturity group V), 'Gordon' (VII), Forrest (V), and Will (III) were the cultivars used as parents. Table 2 shows the crosses used to produce F_2 populations, the years the crosses were made, when F_2 and F_3 generations were grown, and the origin of each parental strain.

Delayed flowering lines with almost the same flowering date were intercrossed. Flowering date is defined here as the number of days from planting to first bloom, first bloom being the appearance of an open flower at any node. This is similar to the R1 stage of the reproductive development defined by Fehr and Caviness (16). Progeny from crosses between delayed flowering lines should indicate whether lines involved in a given cross derived their delayed flowering trait from the same gene(s). The appearance of early flowering in F_1 or F_2 , or a substantial amount of transgressive segregation will suggest that the parents have different gene loci for late flowering.

Crosses were also made between lines with the delayed flowering trait and varieties or lines without that trait.

Table 2: Year crosses were made and when F₂ and F₃ were grown.

Crosses	Year grown		Origin*
	F ₂	F ₃	

1985 crosses			
Crosses between delayed flowering lines			
F85-1027 X F85-369-1	1986	-	1,2
F85-1138 X F84-6291	1986	-	2,1
F85-1226 X F85-562-1	1986	-	2,4A
F85-1028 X F84-6291	1986	-	2,1
F85-1226 X F85-453-1	1986	-	2,3
Crosses between standard varieties or lines and delayed flowering lines			
Will X F85-1138	1986	1987	-,2
Will X F85-1226	1986	1987	-,2
L63-3117 X F85-1138	1986	-	-,2
L63-3117 X F85-1226	1986	-	-,2
Bedford X F85-1138	1986	1987	-,2
Bedford X F85-1313	1986	1987	-,4B
Gordon X F85-1138	1986	-	-,2
Gordon X F85-1313	1986	-	-,4B
1987 crosses			
F85-1226 X F85-1221	1987	-	2,2
Will X F85-1221	1987	-	-,2
Will X F85-1226	1987	-	-,2
Forrest X F85-1221	1987	-	-,2
Forrest X F85-1226	1987	-	-,2
F85-1136 X F85-1138	1987	-	2,2
F85-431 X PI 159925	1987	-	2,-
F85-459 X PI 159925	1987	-	3,-
Bedford X PI 159925	1987	-	-, -
Will X PI 159925	1987	-	-, -

* The first number indicates the cross designation of the female parent (Table 1) and the second that of the male parent.

Crosses made in 1985 are shown in Table 2. The Will X F85-1138 cross was chosen because, Will had flowering date characteristics similar to that of F85-1136, the isoline of F85-1138. In terms of flowering date, this cross may be written: $26 \times (27 + 10)$ where 26 days is Will's previously recorded flowering date, 27 that of F85-1136, and 10 the mean number of days by which F85-1138 is later than F85-1136. Will X F85-1226, L63-3117 X F85-1138, and L63-3117 X F85-1226 were chosen for the same reason as Will X F85-1138; these crosses may be written: $26 \times (28 + 20)$, $27 \times (27 + 10)$, and $27 \times (28 + 20)$, respectively. Twenty-eight days is the flowering time of F85-1221, the isoline of F85-1226; 20 is the number of days by which F85-1226 is later than F85-1221. F85-1136 and F85-1221 flower about the same time as Will. Thus, if delayed flowering results from different genes, segregation ratios for Will X F85-1138 and Will X F85-1226 would likely be different. L63-3117 has the e_2 gene described by Bernard (5). Bedford X F85-1313 and Gordon X F85-1313 were chosen as Bedford and Gordon flower approximately at the same time as F85-1310, the isoline of F85-1313, these crosses may be written: $33 \times (34 + 18)$ and $36 \times (34 + 18)$. Crosses were designed this way to enhance the potential for discrete classes since fewer quantitative genes for flowering date will segregate. Bedford X F85-1138 and Gordon X F85-1138 did not follow the above pattern.

All crosses were made in the field at Gainesville, Florida (29° 40' N). The F_1 plants were grown during the winter in Puerto Rico. The intended population for a genetic analysis of each 1985 cross consisted of 100 to 130 F_2 plants per F_1 plant, 40 plants of each parent, and a limited number of F_1 plants grown within female parent rows.

Additional crosses were made in 1986. These crosses are shown in Table 2. Three categories of crosses were made: 1) Crosses between isoline pairs. These crosses should indicate by how many factors for flowering response an isoline pair differs. F85-1221 and F85-1226 are isolines that are early and late, respectively. F85-1136 and F85-1138 are isolines too, the former being early and the latter late flowering. 2) Crosses between standard varieties and the isoline pair F85-1226, F85-1221. These crosses should indicate the relationship between that isoline pair. 3) Crosses between standard varieties or lines and PI 159925, which should indicate how many genes control the delayed flowering trait of PI 159925. F85-431 and F85-459 were selected because their respective late flowering isoline flowers at the same time as PI 159925. These F_2 population consisted of 112 to 336 plants per cross. Twenty-eight plants were grown of each parent. A limited number of F_1 plants was also planted within female parent rows.

The F_2 plants covering the entire range of flowering dates were selected from Will X F85-1226, Will X F85-1138,

Bedford X F85-1138, and Bedford X F85-1313. Seeds from these plants were planted on 15 June and 19 August 1987. Plants from the 1986 June and August plantings were kept separated. Plants from the June 1986 planting, which were planted in June 1987, occupied 110 plant rows; plants from the August 1986 planting, grown in August 1987, occupied 135 plant rows. Rows were, as for all the 1987 plantings, 2.80m long and 0.90m apart. To facilitate data collection, 28 seeds were planted in each row, and plants were 10cm apart within rows. The evaluation of F_3 will permit us to ascertain F_2 genotypes.

Selections from late-generation segregating rows closely related or from the same parentage as parents with the delayed flowering trait were studied in order to determine whether their segregation ratios were similar to those of corresponding F_2 populations. Furthermore, these rows were tested as some appeared to have segregation patterns different from 3:1 early: late (32). Progenies tested in 1986 and 1987 are shown in Tables 3 and 4, respectively. Seventy eight plant rows were planted in 1986 (July) and 259 plant rows in 1987 (June). For all the 1986 plantings, rows were 3m long and 0.90m apart. Thirty seeds were planted in each row. Plants were 10cm apart within rows.

The 1986 and 1987 plantings were at the Agronomy Farm, University of Florida. The general soil type of the area

Table 3: Source of late-generation parent rows exhibiting apparent segregation for flowering date in 1985.

1985 parent row number	Cross ⁺	Closely relate to	Number of progenies tested in 1986
8209	2	F85-1138	7
8218	2	-	4
8286	4B	-	8
8361	2	F85-1226	5
8363	2	F85-1226	5
8375	2	F85-1027	8
8382	2	-	10
8400	2	-	8
8460	2	-	6
8505	4B	-	6
8514	4B	-	5
8566	2	-	6

⁺ refer to Table 1

Table 4: Parent rows whose progenies were tested in 1987.

1985 parent row number	1986 row number	Number of 1987 progenies examined	Parentage
8210	7124	18	cross 2
8215	7143	4	cross 2
8253	7217	5	cross 2
8253	7222	14	cross 2
8253	7223	7	cross 2
8253	7227	8	cross 2
8253	7232	19	cross 2
8253	7235	14	cross 2
8258	7239	14	cross 2
8258	7243	6	cross 2
8258	7244	16	cross 2
8258	7249	9	cross 2
8258	7253	13	cross 2
8278	7269	19	cross 4B
8278	7271	5	cross 4B
8278	7276	10	cross 4B
8278	7277	22	cross 4B
8278	7278	9	cross 4B
8304	7289	16	cross 2
8304	7294	15	cross 2
8460	--	16	cross 2

was of Arredondo fine sand (a loamy siliceous, hyperthermic, Grossarenic Paleudult). The 1986 field had soybean as the previous crop and corn was the previous crop for the 1987 field. In both years, Lasso (herbicide) was applied at the rate of 4.70 l/ha; Lorsban 4E (4.70 l/ha) was applied for the control of lesser cornstalk borer [Elasmopalpus lignosellus (Zeller)]. The applications were made one day after planting. Fertilization was according to soil tests. Fields were irrigated once before plantings and thereafter as needed.

In 1986, 3 planting dates were used: 3 June, 15 July, and 19 August. Many plants from June 3 plantings died due to damage from lesser cornstalk borer. Furthermore, heavy rains destroyed several seedlings in the July 15 plantings. A third planting date, August 19, was thus adopted for 4 crosses: Will X F85-1138, Will X F85-1226, Bedford X F85-1138, and Bedford X F85-1313. In 1987, 2 planting dates were used: 15 June and 19 August.

Photoperiods (including twilight) were approximately 15h , 14h 40min, and 13h 50min at emergence time on 7 and 19 June, 19 July and 23 August, respectively. June plantings expose plants to the longest photoperiod at Gainesville and August plantings to a significantly shorter photoperiod. June plantings will be referred to as long photoperiod and August plantings as short photoperiod.

Flowering dates were recorded on individual plant every two days.

The minimum family size of populations studied were determined by the methods described by Hanson (19) and Sedecole (40). Chi-square analyses (43) were performed to test goodness-of-fit by populations studied to expected segregation ratios. Chi-square tests for homogeneity (43) were used to test homogeneity within crosses, segregating F_3 rows and parent rows. The t-test was used to compare the mean number of days from planting to flowering of some populations when necessary.

Broad sense heritabilities (H) were estimated by applying the formula $(V_{F_2} - V_{F_1})/V_{F_2}$, where V_{F_1} and V_{F_2} are the variances of the F_1 and F_2 populations of a given cross (10). The "genetic variance", $V_{F_2} - V_{F_1}$, is actually an estimate of the sum of the following variances:

- a) Additive variance;
- b) Variance due to dominance deviations from the additive scheme;
- c) Variance due to the interaction of non-allelic genes.

A maximum estimate of heritability is obtained by this formula. Since few F_1 plants were available, the environmental variance was estimated by the average variance of the two parents, $(V_{P_1} + V_{P_2})/2$, of a given cross. For the same reason dominance deviations were not estimated.

RESULTS AND DISCUSSION

Crosses Among Delayed Flowering Lines

These crosses are tests for allelism. If lines of a given cross derived their delayed flowering trait from different genes, then an unexpected phenotype, i.e. early flowering, should occur in the F_1 or F_2 . Days to flower for parents and F_2 populations are shown in Figures 1a, 1b, 1c, 1d, and 1e. The F_2 of all crosses covered the ranges of the parents in a continuous manner; furthermore, the variability was not greater than that between parents of a given cross. F_1 plants, when available, were similar to the midparent value (Table 5). These results suggest that the parents do not have different genes for delayed flowering.

1986 F_2 Populations

The F_2 populations observed in 1986, in June, July or August plantings, are identified in Table 6. In each cross the female parent (P1) exhibited the standard type flowering response and the male parent (P2) contained the delayed flowering trait transferred from PI 159925. Also presented are the mean days to flower for P1, P2, midparent, F_1 (when available), and F_2 with standard deviation and N values.

There was a decrease in days to first flower as daylength shortened.

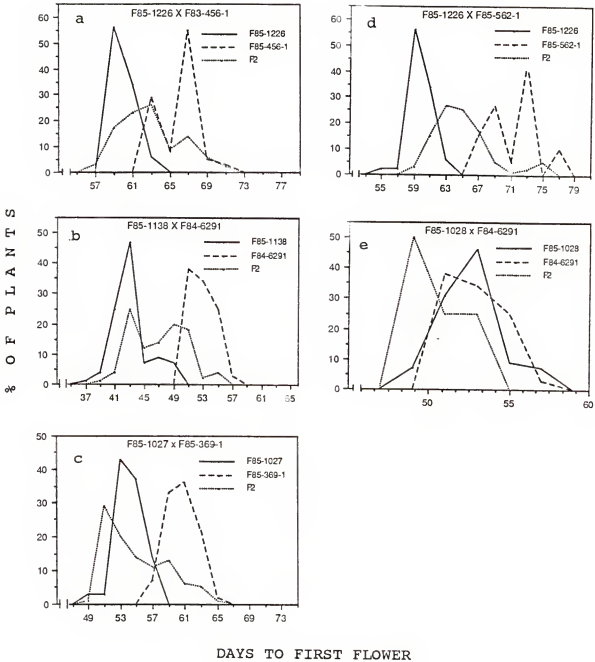


Figure 1: Distribution of days to flower for F_2 populations from crosses between late flowering lines.

Table 5: Parental and hybrid parameters of the crosses between delayed flowering lines.

Cross	Population	Mean days	St. dev.	Range
F85-1226 X F85-456-1	P1	59.8	1.4	55-63
	P2	65.9	2.1	63-71
	P1+P2/2	62.8		
	F ₂	62.9	3.3	57-71
F85-1138 X F84-6291	P1	43.2	2.5	37-49
	P2	52.9	1.7	51-57
	P1+P2/2	48.1		
	F ₂	46.9	3.7	39-55
F85-1027 X F85-369-1	P1	54.1	1.8	49-57
	P2	60.6	1.9	57-65
	P1+P2/2	57.4		
	F ₂	55.0	3.9	49-65
F85-1226 X F85-562-1	P1	59.8	1.4	55-63
	P2	71.3	3.0	67-77
	P1+P2/2	65.5		
	F ₁	65.0		
	F ₂	64.9	3.6	59-75
F85-1028 X F84-6291	P1	54.6	1.4	51-59
	P2	52.9	1.7	51-57
	P1+P2/2	53.7		
	F ₁	53.0		
	F ₂	50.5	2.5	49-53

Table 6: Means of parents, midparents, F_1 , and F_2 for flowering response for the 1986 season

Cross	Population	Mean days	st. dev.	N
June planting				
Will X F85-1138	P1	29.5	1.1	50
	P2	43.2	2.5	73
	P1+P2/2	36.4		
	F_1	31.0		1
	F_2	32.5	3.8	155
Will X F85-1226	P1	29.5	1.1	50
	P2	59.8	1.4	80
	P1+P2/2	44.7		
	F_1	39.0		1
	F_2	42.0	6.4	139
L63-3117 X F85-1138	P1	29.5	1.1	77
	P2	43.2	2.5	73
	P1+P2/2	36.4		
	F_1	31.0		1
	F_2	32.4	4.3	77
L63-3117 X F85-1226	P1	29.5	1.1	77
	P2	59.8	1.4	80
	P1+P2/2	44.7		
	F_1	37.5	1.2	3
	F_2	38.9	8.9	142
Bedford X F85-1138	P1	44.8	2.5	83
	P2	43.2	2.5	73
	P1+P2/2	44.0		
	F_1	41.0		1
	F_2	42.5	10.4	145
Bedford X F85-1313	P1	44.8	2.5	83
	P2	62.5	2.2	78
	P1+P2/2	57.7		
	F_1	49.0		1
	F_2	52.4	4.9	50
Gordon X F85-1138	P1	49.2	1.8	76
	P2	43.2	2.5	73
	P1+P2/2	46.2		
	F_2	41.4	9.5	60

Table 6--continued

Cross	Population	Mean days	st. dev.	N
Gordon X F85-1313	P1	49.2	1.8	76
	P2	62.5	2.2	78
	P1+P2/2	55.9		
	F ₁	47.0		1
	F ₂	52.6	6.1	76
July planting				
Will X F85-1138	P1	29.9	1.6	26
	P2	40.1	1.6	77
	P1+P2/2	35.0		
	F ₁	29.0		1
	F ₂	32.9	4.2	91
Will X F85-1226	P1	29.9	1.6	26
	P2	51.2	2.1	13
	P1+P2/2	40.6		
	F ₂	37.5	5.9	147
L63-3117 X F85-1138	P1	29.7	1.2	17
	P2	40.1	1.6	77
	P1+P2/2	35.0		
	F ₂	34.4	4.5	72
L63-3117 X F85-1226	P1	29.7	1.2	17
	P2	51.2	2.1	13
	P1+P2/2	40.6		
	F ₂	38.4	6.3	53
Bedford X F85-1138	P1	38.3	1.7	33
	P2	40.1	1.6	77
	P1+P2/2	39.2		
	F ₁	39.0		1
	F ₂	42.1	10.3	155

Table 6--continued

Cross	Population	Mean days	st. dev.	N
Bedford X F85-1313	P1	38.3	1.7	33
	P2	52.5	2.3	42
	P1+P2/2	45.4		
	F ₂	45.3	6.8	36
Gordon X F85-1138	P1	37.1	1.2	38
	P2	40.1	1.6	77
	P1+P2/2	38.6		
	F ₂	41.4	9.5	67
Gordon X F85-1313	P1	37.1	1.2	38
	P2	52.5	2.3	42
	P1+P2/2	44.8		
	F ₂	42.2	6.8	75
August planting				
Will X F85-1138	P1	26.7	1.1	58
	P2	34.9	1.4	68
	P1+P2/2	30.8		
	F ₂	27.8	3.8	254
Will X F85-1226	P1	26.7	1.2	58
	P2	43.1	1.1	52
	P1+P2/2	34.9		
	F ₂	33.8	5.0	264
Bedford X F85-1138	P1	30.8	1.2	69
	P2	34.9	1.4	58
	P1+P2/2	32.9		
	F ₂	33.3	5.5	119
Bedford X F85-1313	P1	30.8	1.2	69
	P2	39.4	1.2	66
	P1+P2/2	35.1		
	F ₂	33.5	5.9	120

The F_2 progenies of individual F_1 plants were pooled within each cross and over planting dates after homogeneity tests indicated no significant differences at the 5% level. The F_2 distributions had more plants in the early classes than in late ones; chi-square analyses were done to test fits to 3 early:1 late ratio. The next most logical ratio, 13 early:3 late, which accommodates more early plants was also tested.

In the Will X F85-1138 population, some F_2 segregates flowered as early as the early parent, but, for June planting, none flowered as late as the mean of the late parent. The F_2 distributions were bimodal for two planting dates (Figure 2a). However, discrete classes were obtained only for the July planting. In the absence of discrete classes plants were arbitrarily divided into early and late classes. The divisions were made at low points on the distribution curve. Chi-square analyses showed that segregation for early and late types were in better agreement with 3:1 than 13:3 ratio (Table 7). Plant 1 significantly differed from a 3:1 ratio in July and August. Since the three populations called here plant 1 are from the same F_1 plant, they were pooled to test the fit to 3:1 and 13:3 ratios. The segregation pattern of 213 early:61 late was consistent with a 3:1 ratio (chi-square probability of 0.30-0.20) and with a 13:3 ratio (chi-square probability of 0.20-0.10). These results suggest that the delayed

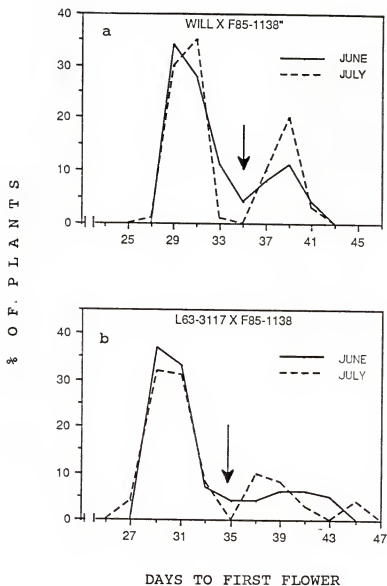


Figure 2: Distribution of days to flower for F_2 populations from crosses having F85-1138 as one parent. Arrows indicate the arbitrary limits between classes.

Table 7 : Observed numbers for early and late flowering classes in each F₂ population of Will X F85-1138 cross and chi-square and homogeneity values.

Pop ⁺	Number of plants		3:1 chi-square		13:3 chi-square	
	Early	Late	Value	P [*]	Value	P
June Planting						
Plant1	57	17	0.16	0.70-0.50	0.86	0.50-0.30
Plant2	62	19	0.11	0.90-0.70	1.18	0.20-0.10
Total	119	36	0.27	0.70-0.50	2.04	0.20-0.10
Homogeneity			0.003	0.95-0.90	0.00	0.99
July Planting						
Plant1	48	26	4.05	0.05-0.01	13.05	<0.001
Plant2	13	4	0.02	0.90-0.70	0.26	0.70-0.50
Total	61	30	3.08	0.10-0.05	12.03	<0.001
Homogeneity			0.99	0.50-0.30	1.05	0.20-0.10
August planting						
Plant1	108	18	7.72	0.01-0.001	1.65	0.20
Plant2	96	32	0.00	0.99	3.29	0.10-0.05
Total	204	50	3.83	0.10-0.05	0.16	0.70-0.50
Homogeneity			3.89	0.05-0.01	4.79	0.05-0.01

+Pop = population

*P = probability

flowering trait maybe due to a single recessive gene (1 locus, 2 alleles) or to a dominant and a recessive gene (2 locus epistatic model). The segregation pattern of F_3 populations, discussed later, will provide data for choosing between alternative hypotheses.

In the L63-3117 X F85-1138 population, F_2 distributions were bimodal for both planting dates. The distribution had two distinct classes for the July planting, whereas arbitrary classes were assigned for the June planting (Figure 2b). For the June planting, the 59 early:18 late F_2 phenotypes were consistent with both 3:1 and 13:3 ratios with chi-square probability of 0.90-0.70 and 0.30-0.20, respectively. For the July planting, the segregation pattern of 54 early:18 late gave better fit to 3:1 ratio better than 13:3 ratio with 0.99 and 0.20-0.10 chi-square probabilities, respectively.

In the 1986 Will X F85-1226 population, discrete classes were obtained only under long-day conditions (Figure 3c). For other planting conditions, arbitrary classes were made (Figures 3a and 3b). Except for the August planting, segregations for early and late types were in better agreement with 3:1 than 13:3 (Table 8).

In the L63-3117 X F85-1226 population, the F_2 distributions were multimodal without discrete classes (Figure 3d and 3e). Segregation for E_2e_2 probably contributed to the failure to obtain discrete classes.

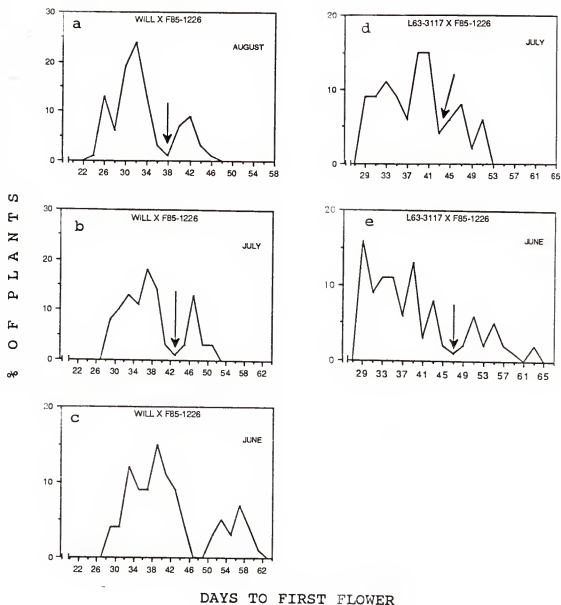


Figure 3: Distribution of days to flower for F_2 populations from 1985 crosses having F85-1226 as one parent. Arrows indicate the arbitrary limits between classes.

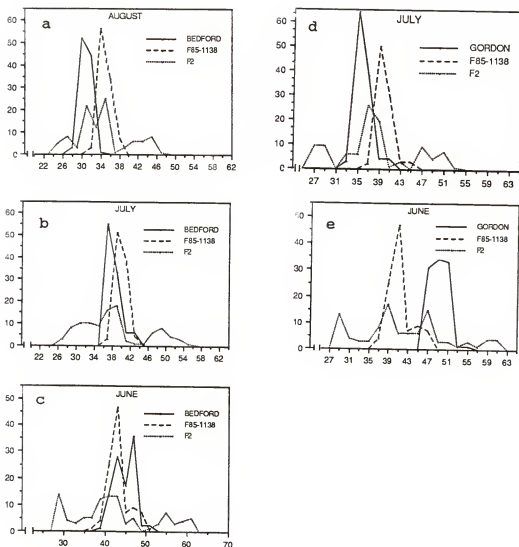
Table 8: Observed numbers for early and late flowering classes in each F₂ population of Will X F85-1226 (grown in 1986) and L63-3117 X F85-1226 and chi-square and homogeneity values.

Pop ⁺	Number of plants		3:1 chi-square		13:3 chi-square	
	Early	Late	Value	P [*]	Value	P
Will X F85-1226						
June planting						
Plant1	61	15	1.12	0.30-0.20	0.14	0.70-0.50
Plant2	62	17	0.13	0.90-0.70	3.23	0.10-0.05
Total	107	32	0.30	0.70-0.50	1.65	0.20-0.10
Homogeneity			0.95	0.50-0.30	1.72	0.20-0.10
July planting						
Plant1	44	18	0.53	0.50-0.30	4.36	0.05-0.01
Plant2	68	17	1.13	0.30-0.20	0.09	0.90-0.70
Total	112	35	0.17	0.70-0.50	2.47	0.20-0.10
Homogeneity			1.47	0.30-0.20	1.98	0.20-0.10
August planting						
Plant1	105	27	1.45	0.30-0.20	0.25	0.70-0.50
Plant2	105	27	1.45	0.30-0.20	0.25	0.70-0.50
Total	210	54	2.90	0.20-0.10	0.50	0.50-0.30
Homogeneity			0.00	0.99	0.00	0.99
L63-3117 X F85-1226						
June planting						
Plant1	60	13	2.01	0.20-0.10	0.04	0.90-0.70
Plant2	55	14	0.81	0.50-0.30	0.10	0.90-0.70
Total	115	27	2.73	0.10-0.05	0.01	0.95-0.90
Homogeneity			0.08	0.90-0.70	0.14	0.90-0.70
July planting						
Plant1	21	6	0.11	0.90-0.70	0.21	0.70-0.50
Plant2	21	5	0.47	0.50-0.30	0.01	0.95-0.90
Total	42	11	0.51	0.50-0.30	0.14	0.90-0.70
Homogeneity			0.07	0.90-.70	0.07	0.90-0.70

+Pop = population *P = probability

Arbitrarily assigned classes fit 13:3 ratio better than 3:1 ratio (Table 8).

In the Bedford X F85-1138 population, the F_2 ranges indicated substantial transgressive segregation in both directions under all planting dates (Figures 4a, 4b, and 4c). Bedford and F85-1138 were characterized by small but significant P2-P1 differences; furthermore, their flowering ranges overlapped. The Gordon X F85-1138 F_2 distribution also showed substantial transgressive segregation in both directions under the two planting dates (Figures 4d and 4e). The separation between parental means was relatively small but significant and their flowering ranges overlapped also. Substantial transgressive segregation should be expected from crosses between parents with nearly equal flowering dates when one parent carries the gene for delayed flowering and the other parent does not. Without the delayed flowering trait, F85-1138 would be identical to its isoline F85-1136 which flowers about 10 days earlier than F85-1138. Thus the introduction of the dominant allele for early flowering, from Bedford, into segregating F_2 plants that otherwise were similar to F85-1138 in flowering date produced the early flowering observed. Also, the introduction of the gene for delayed flowering into F_2 plants that otherwise would flower similar to Bedford produced the late flowering F_2 plants observed. The amount



DAYS TO FIRST FLOWER

Figure 4: Distribution of days to flower for F_2 populations from crosses, having F85-1138 as one parent, whose variation was continuous.

of transgressive segregation in each direction is about the amount of the effect of the gene for delayed flowering.

Another interesting observation from Figure 4 is that in the June planting both Bedford and Gordon flower later than the delayed flowering genotype F85-1138. However, as daylength shortened, from late planting, F85-1138 flowered later than either Bedford or Gordon. Exact amount of the shift can be calculated from data in Table 6. A characteristic of genotypes with the delayed flowering trait appears to be a decreased responsiveness to changes in photoperiod.

In the Gordon X F85-1313 population, the F_2 distributions were bimodal with discrete classes (Figure 5a). For June planting, the segregation pattern of 54 early:22 late was consistent with a 3:1 ratio (chi-square probability of 0.50-0.30) but did not fit a 13 early:3 late ratio (chi-square probability of 0.05-0.01). For July planting, the 55 early:20 late F_2 phenotypes were consistent with a 3:1 ratio (chi-square probability of 0.70-0.50), but not consistent with a 13:3 ratio (chi-square probability of 0.05-0.01).

In the Bedford X F85-1313 population, the F_2 distributions did not have discrete classes at the three plantings (Figure 5b). Arbitrarily assigned classes gave good fit to a 3:1 ratio with chi-square probabilities of 0.50-0.30, 0.95-0.90, and 0.90-0.70 for June, July, and

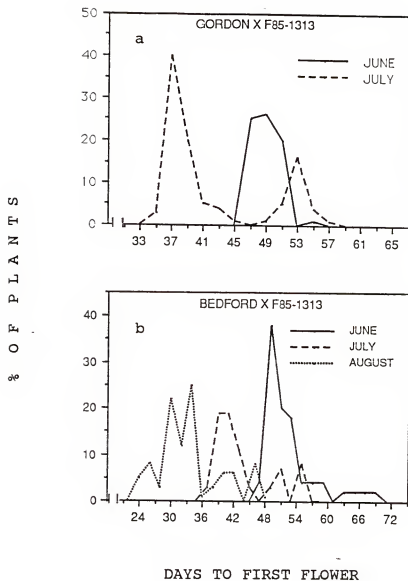


Figure 5: Distribution of days to flower for F_2 populations from crosses having F85-1313 as on parent.

August plantings, respectively. Chi-squares for the goodness-of-fit to a 13:3 ratio were 0.90-0.70, 0.20-0.10, and 0.20-0.10 for June, July, and August plantings, respectively.

The F_2 populations of 1985 crosses, except Bedford X F85-1138 and Gordon X F85-1138 which gave continuous variation, were consistent with both 3 early:1 late ratio and to a lesser extent 13 early:3 late ratio. These results suggest that the delayed flowering trait may be due to either one recessive gene or to a dominant and a recessive gene. These two hypotheses will be discriminated by flowering responses of F_3 populations.

1987 F_3 Data

The segregation patterns of F_2 from crosses between early flowering varieties or lines and late flowering lines were consistent with 3:1 ratios and to a lesser extent to 13:3 ratios. The appearance of early flowering plants in any F_3 row from a late flowering F_2 plant will favor the 2 locus epistatic model over the 1 locus, 2 alleles model.

None of the 51 F_3 plant rows derived from late flowering F_2 plants, from 3 crosses Will X F85-1138, Will X F85-1226, and Bedford X F85-1313, produced early flowering plants. This absence of such plants in the progeny of late F_2 plants indicates that the delayed flowering trait is controlled by a single recessive gene. The F_2 populations grown in 1987 were, therefore, tested for 3:1 ratio only.

The F_3 rows were classified as uniformly early flowering, segregating, and uniformly late flowering. The corresponding inferred F_2 plant genotypes were homozygous early flowering, heterozygous early flowering, and homozygous late flowering.

The F_3 populations of heterozygous early flowering plants were pooled within each cross and over planting date after homogeneity tests indicated no significant differences at the 5% level.

In the Will X F85-1138 F_3 population, under long-day conditions, the row distribution of 4 uniformly early flowering:10 segregating:6 uniformly late flowering was consistent with a 1:2:1 ratio (chi-square probability of 0.70-0.50) (Table 9). This ratio is expected for three genotypes formed by two alleles of a single gene. The analysis of plants in rows that segregated for flowering time gave a moderate fit to 3:1 early:late ratio (chi-square probability of 0.10-0.05). Uniformly early flowering F_3 rows came from F_2 plants that flowered 29 to 31 days after planting (DAP). Segregating rows came from F_2 plants with DAP of 31 to 33. Uniformly late flowering rows came from F_2 plants with DAP of 37 to 41. Under short-day conditions, the row distribution of 13 uniformly early flowering: 8 segregating: 15 uniformly late flowering did not fit 1:2:1 ratio. However, plants in rows which segregated fit a 3:1 ratio (chi-square probability of 0.50-0.30) (Table 10).

Table 9: Analysis of F_2 plant genotypes from three crosses inferred from F_3 rows planted 15 June and 19 August 1987.

Cross and planting date	Number of plants			1:2:1 chi-square	
	H1 ^a	H2	H3	Value	Probability
Will X F85-1138					
June	4	10	6	1.00	0.70-0.50
August	13	8	15	11.34	0.01-0.001
Will X F85-1226					
June	6	11	7	0.40	0.90-0.70
August	10	19	8	0.24	0.90-0.70
Homogeneity				0.52	0.90-0.70
Bedford X F85-1313					
June	4	12	6	0.55	0.90-0.70
August	8	16	9	0.10	0.95
Homogeneity				0.34	0.90-0.70

^aH1 = homozygous early (uniformly early flowering rows)

H2 = heterozygous early (segregating rows)

H3 = homozygous late (uniformly late flowering rows)

Table 10: Analysis of segregating F_3 rows from F_2 plants of four crosses planted 15 June and 19 August 1987.

Cross and planting date	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
Will X F85-1138				
June	115	51	2.89	0.10-0.05
Homogeneity of 10 rows			2.28	0.99-0.95
August	99	38	0.55	0.50-0.30
Homogeneity of 8 rows			9.60	0.20-0.10
Will X F85-1226				
June	151	45	0.44	0.70-0.50
Homogeneity of 11 rows			3.52	0.95-0.90
August	199	62	0.21	0.70-0.50
Homogeneity of 19 rows			8.78	0.99-0.95
Bedford X F85-1138				
June	177	50	1.07	0.30
Homogeneity of 11 rows			6.66	0.90-0.70
August	127	48	0.55	0.50-0.30
Homogeneity of 10 rows			8.33	0.50
Bedford X F85-1313				
June	186	63	0.012	0.95-0.90
Homogeneity of 12 rows			7.56	0.90-0.70
August	225	81	0.35	0.70-0.50
Homogeneity of 16 rows			7.67	0.95-0.90

Uniformly early flowering, segregating and uniformly late flowering F_3 rows came from F_2 plants with DAP of 24 to 28, 28 to 32, and 34 to 38, respectively. These results confirm that the delayed flowering trait found in F85-1138 is due to a single recessive gene.

In the Will X F85-1226 F_3 population, the row distribution pattern was consistent with 1:2:1 uniformly early flowering:segregating:uniformly late flowering under both planting dates (chi-square probability of 0.90-0.70) (Table 9). Chi-square analyses of segregating rows gave good fit to 3:1 ratio, with probability of 0.70-0.50 (Table 10). For the June planting, uniformly early flowering, segregating, and uniformly late flowering rows came from F_2 plants with DAP of 29 to 35, 35 to 45, and 51 to 61, respectively. For the August planting date, uniformly early flowering F_3 rows came from F_2 plants with DAP of 24 to 32, segregating rows from F_2 plants with DAP of 32 to 38, and uniformly late flowering from F_2 plants with DAP of 40 to 46. These data confirm that the delayed flowering trait found in F85-1226 is due to a single recessive gene.

The Bedford X F85-1138 F_3 population was not separated into the 3 categories because its F_2 distribution was continuous. However, F_3 rows with more than one flowering class were analyzed. Under both long- and short-day conditions, plants from segregating rows gave good fits to a 3:1 ratio (Table 10). Segregating rows were of two

categories: rows that were continuous and rows that had two distinct flowering classes. In June, 14 out of 25 segregating rows gave continuous variations whereas, 3 out of 13 were in August. Even though continuous variation and transgressive segregation in both directions were obtained in the F_2 generation, the segregation pattern of F_3 indicates that the delayed flowering trait found in F85-1138 is governed by a single recessive gene.

In the Bedford X F85-1313 population, the row distribution pattern was consistent with 1 uniformly early flowering:2 segregating:1 uniformly late flowering ratio under the two photoperiods (Table 9). Under long days, plants from segregating rows fit a 3:1 ratio (Table 10). Uniformly early flowering, segregating, and uniformly late flowering rows came from F_2 plants with DAP of 47 to 51, 51 to 55, and 57 to 69, respectively. Under short days, plants from segregating rows fit also 3 early:1 late ratio (Table 10). Uniformly early flowering, segregating, and uniformly late flowering rows came from F_2 plants with DAP of 24 to 30, 30 to 36, and 38 to 48, respectively. These results confirm that the delayed flowering trait found in F85-1313 is due to a single recessive gene.

F_2 Populations of 1986 Crosses

As stated earlier, 1986 crosses were designed to determine the genetic difference between isoline pairs and that between PI 159925 and standard varieties and lines.

Table 11 shows the crosses whose F_2 progeny were studied in one or both planting dates. Values for mean days to flower for P_1 , P_2 , midparent, F_1 , and F_2 , and their standard deviations are included. These crosses will be discussed individually in a series of tables and figures to follow.

In Table 11, it is obvious that the relatively few F_1 plants observed generally flowered slightly later than the earlier parent, but earlier than the midparent, suggesting nearly complete dominance for early flowering. This trend was more accentuated under short-day conditions. All crosses represented in June planting were also included in the August planting. The shorter photoperiod for the August planting shortened days to flower in varying amounts, from 3.7 days for F85-1136 to 17 days for F85-431. Two factors appear to have influenced the shorter time to flower: 1) the earlier flowering genotypes within standard or delayed flowering genotypes were shortened less and 2) at any given time to flower, delayed flowering genotypes were shortened less.

In the F85-1226 x F85-1221 population, the F_2 distributions were bimodal with distinct classes under both long- and short-day conditions (Figure 6a). Furthermore, the segregation in early and late plants were not significantly deviating from a 3:1 early:late ratio

Table 11: Means of parents, midparents, F_1 , and F_2 for flowering response for the 1987 season.

Cross	Population	Mean days	st. dev.	N
June Planting				
F85-1226 [*] X F85-1221	P1 ^a	54.1	2.0	63
	P2 ^b	36.1	3.3	56
	P1+P2/2	45.1		
	F_1	40.0	1.2	4
	F_2	44.3	6.4	65
F85-1136 X F85-1138 [*]	P1	29.6	2.4	38
	P2	42.8	1.8	8
Will X F85-1226	P1	30.8	2.0	42
	P2	54.1	2.0	63
	P1+P2/2	42.5		
	F_1	38	1.4	2
	F_2	38.9	6.6	47
Forrest X F85-1226	P1	40.7	2.9	52
	P2	54.1	2.0	63
	P1+P2/2	47.4		
	F_1	42.0	1.4	2
	F_2	43.4	6.6	166
F85-431 X PI 159925 [*]	P1	48.0	1.5	41
	P2	65.3	1.8	24
	P1+P2/2	56.7		
	F_1	48.3	1.0	6
	F_2	52.4	6.2	100
F85-459 X PI 159925	P1	46.8	1.9	29
	P2	65.3	1.8	24
	P1+P2/2	56.1		
	F_1	47.3	.76	7
	F_2	51.3	6.1	47
Bedford X PI 159925	P1	40.3	1.4	3
	P2	65.3	1.8	24
	P1+P2/2	52.8		
	F_1	46.0	1.4	2
	F_2	51.8	7.4	106

Table 11--continued

Cross	Pop.	Mean days	st. dev.	N
August planting				
F85-1226 X F85-1221	P1	46.4	1.7	70
	P2	30.2	2.2	51
	P1+P2/2	38.3		
	F ₁	33.0		1
	F ₂	36.5	5.9	213
F85-1136 X F85-1138	P1	25.9	1.7	58
	P2	36.1	1.1	7
	P1+P2/2	31.0		
	F ₁	26.3	1.2	3
	F ₂	29.4	4.2	19
Will X F85-1226	P1	26.3	2.2	80
	P2	46.4	1.7	70
	P1+P2/2	36.4		
	F ₁	33.0	0.0	2
	F ₂	33.2	6.2	162
Forrest X F85-1226	P1	31.9	1.4	113
	P2	46.4	1.7	70
	P1+P2/2	39.2		
	F ₁	35.0		1
	F ₂	35.7	5.1	224

Table 11--continued

Cross	Population	Mean days	st. dev.	N
F85-431 X PI 159925	P1	31.0	0.5	63
	P2	53.8	4.6	48
	P1+P2/2	42.4		
	F ₁	35.0	0.0	4
	F ₂	38.2	8.5	223
F85-459 X PI 159925	P1	31.4	1.2	50
	P2	53.8	4.6	48
	P1+P2/2	42.6		
	F ₁	36.0	1.4	2
	F ₂	38.6	7.8	116
Bedford X PI 159925	P1	32.3	1.1	40
	P2	53.8	4.6	48
	P1+P2/2	43.1		
	F ₁	37.0		1
	F ₂	38.7	7.8	196
Will X PI 159925	P1	26.3	2.2	80
	P2	53.8	4.6	48
	P1+P2/2	48.1		
	F ₁	31.7	1.2	3
	F ₂	33.7	6.2	212

*F85-1226, F85-1138, and PI 159925 are delayed flowering genotypes

^aP1 = female parent

^bP2 = male parent

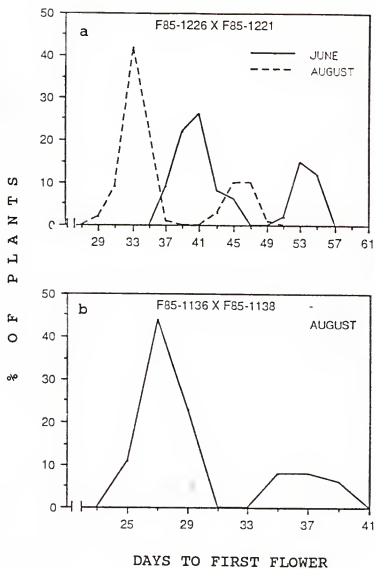


Figure 6: Distribution of days to flower for crosses between isoline pairs.

(Table 12). These results suggest that F85-1221 has one dominant gene for early flowering.

In the F85-1136 X F85-1138 population, too few plants survived lesser cornstalk borer in the June planting for analysis. Under short days, the F_2 distribution was bimodal with distinct classes (Figure 6b). The segregation pattern of 148 early: 42 late was consistent with a 3:1 ratio (chi-square probability of 0.50-0.30) (Table 12). Thus, F85-1136 and F85-1138 differ by one gene, the delayed flowering gene.

Data in Table 11 show that isoline pair F85-1221/1226 differs by more days to flower than isoline pair F85-1136/1138. Much of the interpair difference is associated with the response to photoperiod. However, some of the interpair differences appear to be associated with other unidentified effects. Thus the effect of the gene originally from PI 159925 is dependent upon the length of the photoperiod and may also depend upon other genes in the genetic background.

In the 1987 Will X F85-1226 population, the F_2 distributions had distinct classes under both long- and short-day conditions (Figure 7a and 7b). Chi-square analyses gave good fits to a 3:1 ratio (Table 13). These results indicate that the late flowering trait found in F85-1226 is due to a single recessive gene.

The cross Will X F85-1221 did not produce enough plants for analysis under long-day conditions. Under short days,

Table 12: Observed numbers for early and late flowering classes in each F_2 population of F85-1226 X F85-1221 and F85-1136 X F85-1138 crosses and chi-square and homogeneity values.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
F85-1226 X F85-1221				
June planting				
Plant1	26	9	0.009	0.95-0.90
Plant2	20	10	1.11	0.30-0.20
Total	46	19	0.63	0.50-0.30
Homogeneity			0.49	0.50-0.30
August planting				
Plant1	82	26	0.05	0.90-0.70
Plant2	80	25	0.08	0.90-0.70
Total	162	51	0.13	0.90-0.70
Homogeneity			0.00	0.99-0.95
F85-1136 X F85-1138				
August planting				
Plant1	78	22	0.48	0.50-0.30
Plant2	70	20	0.37	0.70-0.50
Total	148	42	0.85	0.50-0.30
Homogeneity			0.00	0.99-0.95

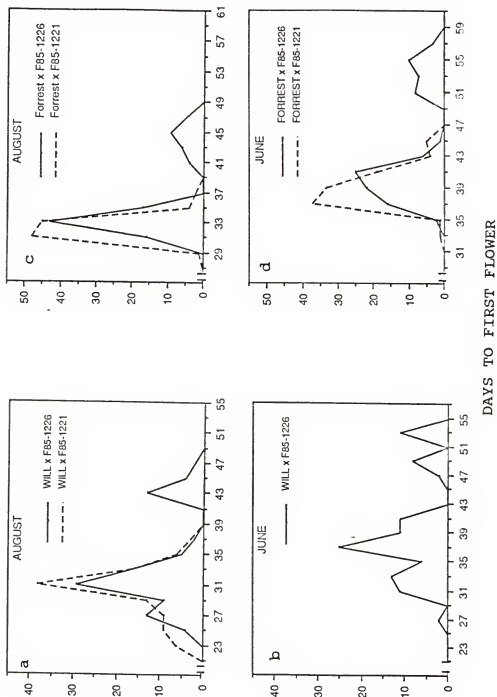


Figure 7: Distribution of days to flower for F_2 populations from crosses between Will and Forrest and the isolate pair F85-1221/1226.

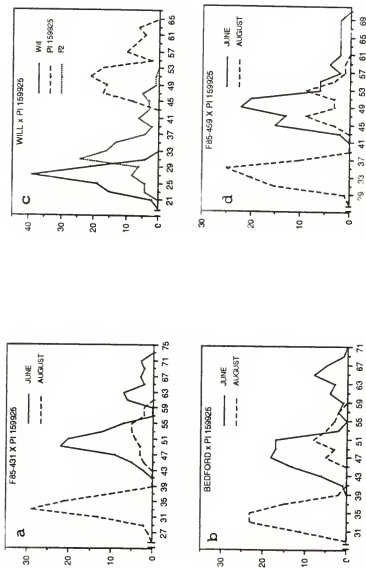
Table 13: Observed numbers for early and late flowering classes in each F_2 population of Will X F85-1226 (grown in 1987) and Forrest X F85-1226 crosses and chi-square and homogeneity values.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
Will X F85-1226				
June planting				
Plant1	18	6	0.00	0.99
Plant2	19	4	0.71	0.50-0.30
Total	37	10	0.35	0.70-0.50
Homogeneity			0.36	0.70-0.50
August planting				
Plant1	54	15	0.40	0.70-0.50
Plant2	72	21	0.30	0.70-0.50
Total	126	36	0.67	0.50-0.30
Homogeneity			0.03	0.90-0.70
Forrest X F85-1226				
June planting				
Plant1	69	22	0.03	0.90-0.70
Plant2	51	24	1.96	0.20-0.10
Total	120	46	0.65	0.50-0.30
Homogeneity			1.34	0.30-0.20
August planting				
Plant1	70	18	0.94	0.50-0.30
Plant2	100	36	0.15	0.70
Total	170	54	0.09	0.90-0.70
Homogeneity			1.00	0.50-0.30

the F_2 distribution was continuous and only covered the early part of the F_2 distribution of the cross Will X F85-1226 (Figure 7a). This result, coupled with that of F85-1221 X F85-1226, confirm that F85-1221 and F85-1226 are isolines differing by one gene; that is, F85-1226 is made of F85-1221 and the gene for late flowering.

In the Forrest X F85-1226 population, the F_2 distributions were bimodal with discrete classes under both long- and short-day conditions (Figure 7c and 7d). The observed number of plants in each class fit a 3:1 ratio with chi-square values ranging from 0.09 to 0.65 and their probabilities varying from 0.30 to 0.90 (Table 13). These results indicate that F85-1226 carries one recessive gene for late flowering that Forrest does not have. In the Forrest X F85-1221 population, under both growing conditions, the F_2 distributions were continuous and only covered the range of the early part of the F_2 distributions of the cross Forrest X F85-1226 (Figure 7c and 7d). These results corroborate the Will X F85-1221 conclusion discussed previously.

In the F85-431 X PI 159925 population, the F_2 distributions were bimodal under both long- and short-day conditions (Figure 8a). PI 159925 is the original source of the late flowering gene; F85-431 is a standard type whose isoline was similar to PI 159925 in days to flower. The F_2



DAYS TO FIRST FLOWER

Figure 8: Distribution of days to flower for F₂ populations from crosses having PI 159925 as one parent.

segregation pattern was consistent with a 3:1 ratio under both photoperiods (Table 14).

In the Bedford X PI 159925 population, the F_2 distributions were almost bimodal with discrete classes under both growing conditions (Figure 8b). Chi-square analyses gave good fits to 3 early:1 late ratio, with probabilities varying from 0.90 to 0.70 (Table 14).

In the F85-459 X PI 159925 population, under long-day conditions, the F_2 distribution was continuous with no transgressive segregation in either direction, and skewed toward earliness (Figure 8d). Under short-day conditions, the F_2 distribution was nearly bimodal with discrete classes. The segregation pattern of 82 early:34 late flowering phenotypes was consistent with a 3:1 ratio (chi-square probability of 0.30-0.20).

In the Will X PI 159925 population, grown only under short-day conditions, the F_2 distribution was continuous with no transgressive segregation and skewed toward earliness (Figure 8c).

Crosses in which PI 159925 was one of the parents were consistently in agreement with a 3 early:1 late ratio, indicating that the delayed flowering trait found in PI 159925 is due to a single recessive gene. Hartwig and Kihl (24) suggested that as many as three genes were involved in the control of the delayed flowering trait of PI 159925; in addition, they found delayed flowering to

Table 14: Observed numbers for early and late flowering classes in each F_2 population of F85-431 X PI 159925 and Bedford X PI 159925 crosses and chi-square and homogeneity values.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
F85-431 X PI 159925				
June planting				
Plant1	32	2	6.62	0.01-0.001
Plant2	29	10	0.01	0.95-0.90
Plant3	22	5	0.60	0.50-0.30
Total	83	17	3.41	0.10-0.05
Homogeneity			3.82	0.20-0.10
August planting				
Plant1	48	19	0.40	0.50-0.30
Plant2	45	17	0.20	0.70-0.50
Plant3	75	19	1.15	0.30-0.20
Total	168	55	0.01	0.90
Homogeneity			1.74	0.70-0.50
Bedford X PI 159925				
June planting				
Plant1	44	14	0.02	0.90-0.70
Plant2	36	12	0.00	0.99
Total	80	26	0.01	0.90
Homogeneity			0.01	0.90
August planting				
Plant1	80	23	0.40	0.70-0.50
Plant2	66	27	0.80	0.50-0.30
Total	146	50	0.03	0.90-0.70
Homogeneity			1.17	0.30-0.20

behave as a recessive. This discrepancy may be explained by the fact that Hartwig and Kiihl were more concerned with the utilization of the delayed flowering trait in a moderate size breeding program than with the inheritance of the trait.

Bernard (5) described two independent gene pairs, E_1e_1 and E_2e_2 , which affect time of flowering and maturity in soybeans. The gene pair described in this study is different from the two gene pairs, E_1e_1 and E_2e_2 , in that the early allele is nearly completely dominant in this study; whereas, the late allele at each locus is partially dominant in the Bernard's study.

Heritability values for flowering date (Table 15) were generally large, which is in agreement with other heritability estimates for this trait (3, 28).

1986 Progeny Tests of Late-generation Rows

For the 1986 and 1987 progeny tests, progenies were pooled within each parent row after homogeneity chi-squares indicated no significant differences at the 5% level.

In the 1986 progeny tests, rows from parent row numbers 8218, 8286, 8382, and 8400 were either early uniform, late uniform, or segregating but continuous with no transgressive segregation nor definite low points. These parent rows were not considered in the analyses.

Two types of segregation patterns were observed: 3 early:1 late and 1 early:3 late, the former being more

Table 15: Heritability estimates in percent

Cross	H		
	June	July	August
1986 season			
F85-1226 X F85-456-1	71	-	-
F85-1138 X F84-6291	67	-	-
F85-1027 X F85-369-1	77	-	-
F85-1226 X F85-562-1	58	-	-
F85-1028 X F84-6291	61	-	-
Will X F85-1138	74	85	89
Will X F85-1226	96	89	94
L63-3117 X F85-1138	80	90	-
L63-3117 X F85-1226	98	92	-
Bedford X F85-1138	97	97	94
Bedford X F85-1313	77	91	95
Gordon X F85-1138	94	97	-
Gordon X F85-1313	89	92	-
1987 season			
F85-1226 X F85-1221	81	-	88
Forrest X F85-1226	85	-	90
Will X F85-1226	95	-	90
F85-431 X PI 159925	92	-	85
F85-459 X PI 159925	90	-	81
Bedford X PI 159925	95	-	81
Will X PI 159925	-	-	89
F85-1136 X F85-1138	-	-	88

common. The 3 early:1 late ratio was obtained in progeny rows of early plants from parent rows, the late plants of parent rows bred true. The 1 early:3 late ratio was obtained in rows grown from late plants of parent rows, the early plants of parent rows bred true. In the following discussion, parent row will be referred to as line.

In the progeny of line 8209, the segregation pattern of 80 early:22 late was consistent with a 3:1 ratio (chi-square probability of 0.50-0.30) (Table 16). These results are in agreement with those obtained in some crosses where F85-1138, a close relative of line 8209 (table 3), was one of the parents. That is, the late flowering trait of F85-1138 is due to a single recessive gene. Early and late classes differ by 10.7 days, a difference similar to that for F85-1136 and F85-1138.

The progeny of line 8361 fit a 3:1 ratio with chi-square probability of 0.70-0.50 (Table 16). Thus, line 8361, a close relative of F85-1226 (Table 3), provides additional evidence that the delayed flowering trait found in F85-1226 is due to a recessive gene.

Line 8363, a close relative of F85-1226 (Table 3), gave progenies that fit a 3 early:1 late ratio with chi-square probability of 0.95 (Table 16). Thus, as for F85-1226, the late flowering segregates from lines 8361 and 8363 are inherited as a simple recessive. Early and late classes of lines 8361 and 8363 differ by 13.6 and 13.5 days,

Table 16: Segregation of parent rows 8209, 8361, and 8363 tested in 1986.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
Line 8209				
Plant1 ^a	30	10	0.00	0.99
Plant2	14	3	0.49	0.50-0.30
Plant3	12	5	0.17	0.70-0.50
Plant4	15	4	0.16	0.70-0.50
Total	80	22	0.64	0.50-0.30
Homogeneity			0.18	0.99-0.95
Line 8361				
Plant1	33	10	0.07	0.90-0.70
Plant2	9	5	0.85	0.50-0.30
Plant3	28	12	0.53	0.50-0.30
Total	70	27	0.41	0.70-0.50
Homogeneity			1.04	0.70-0.50
Line 8363				
Plant1	37	11	0.11	0.90-0.70
Plant2	22	9	0.27	0.70-0.50
Total	59	20	0.004	0.95
Homogeneity			0.38	0.70-0.50

^aPlant = progeny of a single plant of a line

respectively. These differences are smaller than the difference between F85-1221 and F85-1226. The dissimilarity observed may be due to different genetic background.

Line 8375, a close relative of F85-1027 (Table 3), produced progenies that fit a 3:1 ratio (Table 17). F85-1027, therefore, has an inheritance pattern similar to that of F85-1138 and F85-1226.

Line 8505, a descendent of cross 4B (Table 3), produced progenies that fit a 3:1 ratio with chi-square probability of 0.90-0.70 (Table 17). The delayed flowering trait found in line 8505 behaves as a simple recessive.

Line 8566, a close relative of F85-300-1 (Table 3), produced progenies that fit a 3 early:1 late ratio with chi-square probability of 0.70-0.50 (Table 17). Thus, F85-300-1 evidently derived its delayed flowering trait from PI 159925.

For line 8460, a descendent of cross 2, the segregation pattern of 14 early:48 late was consistent with a 1:3 ratio (chi- probability of 0.70-0.50). This distribution indicates that lateness is dominant over earliness. The analysis of F_3 lines had ruled out the possibility of the delayed flowering trait of PI 159925 being due to a recessive and a dominant gene as well. Furthermore, the low frequency of the 1:3 ratio excludes the 13:3 ratio. This dominant gene for late flowering found in line 8460 is not,

Table 17: Segregation of parent rows 8375, 8505, and 8566 tested in 1986.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
Row 8375				
Plant1 ^a	32	10	0.03	0.90-0.70
Plant2	16	3	0.85	0.50-0.30
Plant3	17	4	0.40	0.70-0.50
Plant4	13	5	0.08	0.90-0.70
Total	78	22	0.48	0.50-0.30
Homogeneity			0.88	0.90-0.70
Row 8505				
Plant1	29	6	1.16	0.30-0.20
Plant2	31	10	0.01	0.95-0.90
Plant3	15	9	2.00	0.20-0.10
Plant4	10	2	0.44	0.70-0.50
Total	85	27	0.05	0.90-0.70
Homogeneity			3.55	0.50-0.30
Row 8566				
Plant1	42	10	0.92	0.50-0.30
Plant2	31	11	0.03	0.90-0.70
Plant3	21	6	0.11	0.90-0.70
Total	94	27	0.41	0.70-0.50
Homogeneity			1.04	0.70-0.50

^aPlant = progeny of a single plant of a line

therefore, from PI 159925. Its source may be one of the parents, but D77-12480, used in cross 2.

The 1986 progeny tests show that the delayed flowering trait is due to a single recessive gene. However, another gene different from that of PI 159925 controls late flowering, this latter gene behaves as a simple dominant.

1987 Progeny Tests of Late-generation Rows

In 1987, progenies of lines 8210-7124 (the first number is the 1985 parent row and the second the 1986 parent row), 8258-7239, 8258-7244, 8278-7271, and 8278-7277 fit a 3:1 ratio with chi-square probability varying from 0.05-0.90 (Table 18). Segregating rows were produced by early plants of parental lines; late plants of parental lines bred true. These results indicate that the delayed flowering character found in these populations is controlled by a single pair of recessive alleles.

Progenies of line 8278-7269, a descendent of cross 4B (Table 4), fit a 1 early:2 intermediate:1 late ratio. Because of the discrepancy in the limit between early and late classes, the two populations from this line were not pooled. For population 1, the segregating pattern of 4 early:8 intermediate:4 late was consistent with a 1:2:1 ratio (chi-square probability of 0.99). Early and intermediate classes differed by 6 days and intermediate and late classes by 4 days. For population 2, the

Table 18: Segregation of parent rows 8210-7124, 8258-7239, 8258-7244, 8278-7271, and 8278-7277 progeny tested in 1987.

Population	Number of plants		3:1 chi-square	
	Early	Late	Value	Probability
Parent row 8210-7124				
plant1	20	3	1.76	0.20-0.10
plant2	14	12	6.20	0.05-0.01
plant3	18	7	0.12	0.90-0.70
plant4	19	3	1.52	0.300-0.20
plant5	19	8	0.31	0.70-0.50
plant6	29	10	0.008	0.95-0.90
plant7	22	5	0.60	0.50-0.30
total	141	48	0.016	0.90
homogeneity			10.50	0.20-0.10
Parent row 8258-7239				
plant1	7	3	0.13	0.70-0.50
plant2	12	3	0.03	0.90-0.70
plant3	16	3	1.28	0.30-0.20
plant4	16	7	0.36	0.70-0.50
plant5	16	9	1.61	0.30-0.20
plant6	13	9	2.97	0.10-0.05
plant7	14	5	0.06	0.90-0.70
total	94	39	1.32	0.30-0.20
homogeneity			5.12	0.70-0.50
Parent row 8258-7244				
plant1	20	4	0.89	0.50-0.30
plant2	20	2	2.97	0.10-0.05
plant3	17	5	0.07	0.90-0.70
total	57	11	2.83	0.10-0.05
homogeneity			1.10	0.70-0.50
Parent row 8278-7271				
plant1	17	5	0.07	0.90-0.70
plant2	13	6	0.44	0.70-0.50
plant3	13	8	1.92	0.20-0.10
total	43	19	1.05	0.30-0.20
homogeneity			1.38	0.50
Parent row 8278-7277				
plant1	12	8	2.40	0.20-0.10
plant2	14	6	0.27	0.70-0.50
plant3	13	6	0.44	0.50-0.30
total	39	20	2.49	0.20-0.10
homogeneity			0.62	0.90-0.70

segregation pattern of 3 early:11 intermediate:4 late was consistent with 1:2:1 ratio (chi-square probability of 0.70-0.50). Early and intermediate classes differed by 6 days and intermediate and late classes by 4 days. These two populations were produced by early plants of the parental line. This is probably a case of incomplete dominance, the heterozygote being different from either extreme. However, because of small number of plants (expected early and late classes were fewer than 5), further studies are needed to ascertain the genotype of each class.

In the progenies of line 8304-7289, a descendent of cross 2 (Table 4), the segregation pattern of 38 early:92 late was consistent with a 1:3 ratio with chi-square probability of 0.30-0.20 (Table 19). Segregating rows were produced by late plants of the parental line, early plants from the parental line bred true. This is evidence that another gene for late flowering, different from that of PI 159925, exists in the genetic stocks under investigation.

Progenies of line 8460 were progeny tested in 1987. The segregation pattern of 21 early:56 late was consistent with 1:3 ratio with chi-square probability of 0.70-0.50 (Table 19). Segregating rows were produced by late plants of parental line, early plants of parental line bred true. This suggests the existence of another gene for late flowering different from that of PI 159925 in the genetic stocks being investigated.

Table 19: Segregation of parent rows 8304-7289
and 8460 progeny tested in 1987.

Population	Number of plants		1:3 chi-square	
	Early	Late	Value	Probability
Parent row 8304-7289				
plant1	8	17	0.65	0.50-0.30
plant2	2	22	3.56	0.10-0.05
plant3	5	14	0.06	0.90-0.70
plant4	6	10	1.33	0.30-0.20
plant5	7	15	0.55	0.50-0.30
plant6	10	14	3.56	0.10-0.05
total	38	92	1.24	0.30-0.20
homogeneity			8.97	0.20-0.10
Parent row 8460				
plant1	4	21	1.09	0.30-0.20
plant2	10	18	1.72	0.20-0.10
plant3	7	17	0.23	0.70-0.50
total	21	56	0.21	0.70-0.50
homogeneity			2.83	0.30-0.20

The 1987 progeny tests of segregating rows confirm the hypothesis that flowering trait found in PI 159925 is controlled by a single recessive gene pair. A dominant gene for late flowering, not from PI 159925, exists in the genetic stocks studied. The E_1 gene is common in varieties adapted to southern U.S. (6); thus, this other gene could be E_1 from Kirby or Forrest. However, in the development of isoline pairs described earlier, the selection process should have eliminated E_1 . An allelism test should be done between lines considered to have the flowering response of the dominant late flowering gene described in this study and lines considered to have the flowering response of E_1 .

SUMMARY AND CONCLUSIONS

Inheritance of delayed flowering trait was studied in 1986 and 1987. Nine lines with the delayed flowering trait (F85-1226, F85-1138, F85-1313, F85-1027, F85-1028, F85-369-1, F85-453-1, F84-6291, and PI 159925) were either intercrossed or crosses with lines without the delayed flowering trait. The F_1 , F_2 , and F_3 populations and the progenies of segregating rows related to lines with the delayed flowering trait used as parents were studied.

Based on the studies conducted, the following may be inferred:

a. The genetic control of flowering time under long- (15h) and short-day (13h 50min) conditions is not different. However, the degree of dominance is slightly influenced by the daylength.

b. The segregation of F_2 populations, except those of Will X PI 159925, Bedford X F85-1138, and Gordon X F85-1138, were in good agreement with the phenotypic ratio 3 early:1 late expected for recessive, single-gene inheritance. Furthermore, the distributions of phenotypes of F_3 families also conformed to the pattern expected for recessive, single-gene inheritance. All late F_2 plants bred true, while early F_2 plants produced early uniform and segregating

rows; in segregating rows, plant phenotypes were in agreement with a 3 early:1 late ratio. The delayed flowering trait transferred from PI 159925 is, therefore, controlled by a single pair of recessive alleles.

c. Evidence was found for the existence of a single, dominant gene for late flowering in the genetic stocks being investigated. Progenies of lines 8304-7189 and 8460 were consistent with the phenotypic ratio 1 early:3 late expected for dominant, single-gene inheritance for lateness. This other gene appears not to be from PI 159925 since it was not expressed in F_3 populations of lines which derived their delayed flowering gene from PI 159925. Furthermore, it was not common in the progeny of late-generation rows. Thus, in late generations, genes for late flowering contributed by lines other than PI 159925 may be expressed, giving the impression that PI 159925 has more than one factor for the delayed flowering response. Line 8304-7189 and line 8640 are both descendents of cross 2. One of the parents in that cross, other than D77-12480, may be the source of the other gene for late flowering.

APPENDIX

Table 20: Frequency distribution of parents, F_1 and F_2 progeny of crosses among delayed flowering genotypes.

Days from planting to 1st flower	P1*	P2	F ₁	F ₂	
				plant1	plant2
A F85-1226 X F85-456-1					
55	1				
57	1				3
59	46			2	14
61	27			4	17
63	5	11		8	16
65	0	3		5	3
67		21		5	8
69		2		2	3
71		1		1	1
B F85-1138 X F84-6291					
37	1				
39	3			1	
41	18			5	
43	34			16	15
45	5			9	6
47	7			9	8
49	5			1	24
51	0	26		19	3
53		24		1	1
55		17		2	3
57		2			
C F85-1027 X F85-369-1					
49	1			0	1
51	1			34	14
53	15			23	11
55	14			14	10
57	5	3		2	16
59	0	15		3	18
61		16		0	10
63		10		0	9
65		1		1	1

Table 20--continued

Days from planting to 1st flower	P1	P2	F ₁	F ₂	
				plant1	plant2
D F85-1226 X F85-5621					
55	1				
57	1				
59	46			2	2
61	27			10	8
63	5			21	11
65	0		1	11	19
67		6		7	14
69		10		1	5
71		2		0	1
73		17		1	2
75		0		4	2
77		4			
E F85-1028 X F84-6291					
49	3			31	50
51	14	26		15	25
53	21	24	1	25	15
55	4	17			
57	3	2			

*P1 refers to the female parent and P2 to the male parent

Table 21: Frequency distribution of Will (P1), F85-1138 (P2), F₁, and F₂ for flowering periods under three planting dates.

D ^a	June					July					August			
	P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂		P1	P2	F ₂	
				A ⁺	B ⁺				A	B			A	B
24											1		26	6
25														
26											36		62	64
27						3			1					
28											20		17	24
29	39			37	15	10		1	21	6				
30											1		3	2
31	9		1	25	28	11			25	7				
32												2	5	6
33	2			2	15	2			1	0				
34												38	9	14
35				0	7				0	0				
36												23	2	11
37		1		4	9		2		8	1				
38												5	2	1
39		3		10	7		40		16	2				
40														
41		18		3	3		29		2	1				
42														
43		34					3							
44														
45		5					3							
46														
47		7												
48														
49		5												

^aD = days from planting to first flower

⁺A = plant1

⁺B = plant2

Table 22: Frequency distribution of L63-3117 (P₁), F85-1138 (P₂), F₁, and F₂ for flowering periods under two planting dates.

D ^a	June				July		
	P ₁	P ₂	F ₁	F ₂	P ₁	P ₂	F ₂
27							3
29	36			28	12		23
31	9		1	25	4		22
33	2			6	1		6
35	0			3			0
37		1		3		3	7
39		3		3		40	6
41		18		5		29	2
43		34		4		3	0
45		5		0		3	3
47		7					
49		5					

^aD = Days from planting to first flower

Table 23: Frequency distribution of Will (P1), F85-1226 (P2), and F₂ for flowering periods under three planting dates.

D*	June					July					August				
	P1	P2	F ₂			P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂	
			F ₁	A ⁺	B [*]				A	B				A	B
24												1		1	1
25															
26												36		16	17
27							3								
28												20		9	6
29	39			3	3	10			3	9					
30												1		17	32
31	9			4	1	11			8	7					
32												0		29	24
33	2			5	11	2			7	12					
34														19	15
35	0			5	8				6	10					
36														3	6
37				12	1				10	16					
38														1	1
39			1	11	9				8	12					
40													2	5	14
41				10	5				2	3					
42													21	17	7
43				7	6				2	0					
44													28	4	5
45				4	2				3	2					
46													1	1	0
47				0	0				12	6					
48															
49				0	0		4		4	3					
50															
51				0	4		6		3	1					
52															
53				6	1		1								
54															
55		1		0	4		2								
56															
57		1		6	4		0								
58															
59		46		2	4										
60															
61		27		1	0										
62															
63		5													

*D =days to first flower *A=plant1 *B=plant2

Table 24: Frequency distribution of L63-3117 (P1), F85-1226 (P2), F₁, and F₂ for flowering periods under two planting dates.

D ^a	June					July			
	P1	P2	F ₁	F ₂		P1	P2	F ₂	
				A ⁺	B [*]			A	B
29	36			8	15	12		2	3
31	9			8	5	4		4	1
33	2			8	8	1		2	4
35	0			7	9	0		2	3
37			2	5	4			1	2
39			1	12	7			5	3
41				2	2			4	4
43				9	3			1	1
45				1	1			2	1
47				0	1			3	1
49				1	1		4	1	0
51				4	4		6	3	3
53				0	3		1		
55		1		3	4		2		
57		1		3	0		0		
59		46		0	1				
61		27		0	0				
63		5		2	1				

^aD = days from planting to first flower

⁺A = plant1

^{*}B = plant2

Table 25: Frequency distribution of Bedford (P1), F85-1138 (P2), F₁, and F₂ for flowering periods under three planting dates.

D ^a	June					July					August			
	P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂
				A ⁺	B ⁺				A	B				A
24														6
25														
26														10
27										5				
28											2			4
29				15	7				10	2				
30											36			27
31				0	6				8	7				
32											30	2		14
33				1	4				3	12				
34											1	38		30
35				2	6				10	3				
36												23		1
37		1		5	4	18	2		9	13				
38												5		3
39	1	3		8	11	11	40	1	13	14				
40														7
41	12	18	1	14	6	2	29		1	2				
42														7
43	23	34		7	13	2	3		2	0				
44														9
45	15	5		2	0		3		1	1				
46														1
47	30	7		6	2				4	5				
48														
49	2	5		0	0				7	5				
50														
51	2	0		0	1				3	3				
52														
53				2	2				1	4				
54														
55				5	6				1	1				
56														
57				2	3									
58														
59				3	4									
60														
61				4	5									

^aD = days from planting to first flower

⁺A = plant1 ⁺B = plant2

Table 26: Frequency distribution of F85-1138 (P1), Gordon (P2), and F₂ for flowering periods under two planting dates.

D ^a	June			July		
	P1	P2	F ₂	P1	P2	F ₂
27						6
29			9			6
31			3			0
33			2		1	4
35			2		3	4
37	1		6	2	30	17
39	3		12	40	3	12
41	18		4	29	1	1
43	34		4	3		3
45	5		4	3		0
47	7	23	11			6
49	5	26	2			3
51		25	2			5
53		1	1			1
55		1	2			
57			1			
59			3			
61			3			

^aD = days from planting to first flower

Table 27: Frequency distribution of Bedford (P1), F85-1313 (P2), F₁, and F₂ for flowering periods under three planting dates.

D ^a	June				July				August			
	P1	P2	F ₁	F ₂	P1	P2	F ₁	F ₂	P1	P2	F ₁	F ₂
24												6
25												
26												10
27												
28									4			4
29												
30									36			27
31												
32									30			14
33												
34									1			30
35												
36										1		1
37					18			1				
38										21		3
39	1				11			7				
40										41		7
41	12				2			7				
42										3		7
43	23				2			7				
44												0
45	15							4				
46												9
47	30			2		1		1				
48												1
49	2		1	19		2		0				
50												
51	2			10		12		1				
52												
53				9		22		2				
54												
55				2		1		0				
56												
57		1		2		2		2				
58												
59		8		2		2		2				
60												
61		26		0								
63		20		1								
65		20		1								
67		3		1								
69				1								

^aD = days from planting to first flower

Table 28: Frequency distribution of Gordon (P₁), F85-1313 (P₂), F₁, and F₂ for flowering periods under two planting dates.

D ^a	June				July		
	P ₁	P ₂	F ₁	F ₂	P ₁	P ₂	F ₂
33					1		
35					3		2
37					30		30
39					3		15
41					1		4
43							3
45							1
47	23		1	19		1	0
49	26			20		2	1
51	25			15		12	4
53	1			0		22	11
55	1			1		1	3
57		1		0		2	1
59		8		1			2
61		26		15			
63		20		3			
65		3		3			

^aD = days from planting to first flower

Table 29: Frequency distribution of segregating F_3 row from Will X F85-1138 for flowering periods.

D*	23	25	27	29	31	33	35	37	39	41	43
June											
A*				3	5	3	0	0	0	7	1
B				1	6	5	3	0	0	3	1
C				1	1	2	1	0	0	2	0
D			3	7	4	1	0	0	0	6	1
E				4	5	2	0	0	0	4	1
F			2	5	5	3	0	0	0	4	2
G				4	3	0	0	0	0	3	0
H			3	2	4	2	1	0	0	2	3
I			2	3	3	2	0	0	0	3	2
J			1	5	4	2	0	0	0	4	2
August											
K		1	7	3	0	0	2	3			
L	1	3	7	1	2	0	2	1			
M		1	9	2	2	0	0	2			
N	2	1	3	2	2	0	1	4	3		
O		1	2	7	5	0	0	0	2		
P	1	1	4	7	5		0	2	6		
Q		3	5	2	0	0	5	2			
R			4	2	1	0	0	3			

aD = days from planting to first flower

*A = row from a single plant from a late-generation row

Table 30: Frequency distribution of segregating F₃ rows from Will X F85-1226 for flowering periods.

D^a 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55

June

A*								1	5	6	3	1	0	0	1	4
B		4	1	0	1	3	7	0	0	0	0	0	0	1	1	3
C			2	0	2	5	6	2	0	0	0	0	0	3	1	1
D							3	3	1	0	0	1	1			
E		1	2	0	3	4	2	7	2	0	0	0	2	1		
F				1	1	2	2	4	1	0	0	0	0	3	1	
G	1	2	0	1	3	2	3	2	0	0	0	2	1	1		
H			2	1	3	1	1	0	1	0	0	1				
I			2	1	1	4	2	4	0	0	1	5				
J						2	4	6	2	1	0	0	1	4	1	
K								5	4	1	1	0	0	1	2	1

August

L	1	4	2	0	2	1	0	0	0	5						
M					2	10	0	0	0	2	1					
N					2	3	0	0	0	1	0	2				
O					4	7	0	0	0	1	0	3				
P			1	2	13	0	0	0	5							
Q			1	4	2	0	0	0	1							
R		1	2	8	3	0	0	0	0	0	1					
S					5	0	0	0	0	0	1					
T		1	1	3	2	0	0	0	0	1						
U				9	5	0	0	0	0	0	1	4				
V			1	3	3	3	0	0	0	0	0	2				
W				5	2	0	0	0	0	0	1	2				
X				3	0	0	0	0	0	0	0	0	1			
Y				7	6	2	0	0	0	0	1	3				
Z				2	7	2	0	0	0	0	2	2				
AA				13	1	0	0	0	0	0	2	1				
AB				2	4	6	0	0	0	0	2	5	1			
AC	1	2	5	5	2	0	0	0	0	0	1	0	1			
AD	2	0	4	6	3	0	0	0	0	0	2	1	1			

^aD = days from planting to first flower

^aA = row from a single plant from a late generation row

Table 31: Frequency distribution of segregating F₃ rows from Bedford X F85-1313 for flowering periods.

D^a 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55

June

A*																	
B																	
C																	
D																	
E																	
F																	
G																	
H																	
I																	
J																	
K																	
L																	

August

M																	
N																	
O																	
P																	
Q																	
R																	
S																	
T																	
U																	
V																	
W																	
X																	
Y																	
Z																	
AA																	
AB																	

^aD = days from planting to first flower

^aA = row from a single plant from late-generation row

Table 32: Frequency distribution of parents and hybrids of two crosses between isoline pairs for flowering periods under two planting dates.

	June					August				
				F ₂					F ₂	
D ^a	P1	P2	F ₁	A ⁺	B ⁺	P1	P2	F ₁	A	B
A F85-1226 X F85-1221										
23								1		
25								3		
27		3						2		
29		3						10	4	1
31		2						29	4	15
33		0						5	3	39
35		8						1	33	50
37		25		6	9				2	14
39		15	2	10	4				0	0
41			2	10	7				0	0
43				3	2	7			0	0
45				3	1	15			12	7
47				0	0	41			12	9
49				0	0	6			2	9
51	12			0	1	1				
53	14			5	5					
55	29			4	4					
57	6									
59	2									
B F85-1136 X F85-1138										
23						8				
25						20		1	11	11
27						26		2	45	38
29						3			22	21
31						1			0	0
33									0	0
35							4		8	7
37							5		9	7
39									5	6

^aD = days from planting to first flower

⁺A = plant1

⁺B = plant2

Table 33: Frequency distribution of Will X 1226/1221 for flowering periods under two planting dates.

D ^a	June					August				
	P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂	
				A ⁺	B ⁺				A	B

A Will X F85-1226

21						2				
23						11				
25						14			9	4
27	2			1		29			8	12
29	12			0		16			5	8
31	20			5		3			19	27
33	4			2	4			2	13	14
35				2	1				0	0
37				1	4				0	2
39				1	4				9	0
41				0	5				0	0
43				0	0			7	2	12
45				0	0			15	1	3
47				0	1			41	3	4
49				3	1			6	0	2
51		12		0	0			1		
53		14		3	2					
55		29								
57		6								
59		2								

B Will X F85-1221

23						1		2
25						5		3
27						2	1	3
29						10	1	4
31						25		12
33						5		5
35						1		2
37								1

^aD = days from planting to first flower⁺A = plant1⁺B = plant2

Table 34: Frequency distribution of Bedford (P1), PI 159925 (P2), F₁, and F₂ for flowering periods under two planting dates.

D ^a	June					August				
	P1	P2	F ₁	F ₂		P1	P2	F ₁	F ₂	
				A ⁺	B ⁺				A	B
31						15			14	7
33						24			29	17
35						1			23	22
37								1	12	18
39	15								2	2
41	14				1				0	0
43	4			3	3				0	0
45			1	6	7				0	0
47			1	11	8		4		2	8
49				12	8		8		3	2
51				12	7		6		9	6
53				0	2		10		4	6
55				0	0		8		2	4
57				2	0		2		3	1
59				0	1		5			
61		1		4	0		2			
63		5		3	2		3			
65		7		4	4					
67		11		0	5					
69				1						

^aD = days from planting to first flower

⁺A = plant1

⁺B = plant2

Table 35: Frequency distribution of late-generation rows
8304-7289 and 8460 for flowering periods under
long day-conditions.

D ^a	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57
8304-7289															
A ⁺	3	3	2	0	0	0	8	4	4	1					
B		1	1	0	0	0	12	4	4	2					
C	5	0	0	0	0	0	8	4	2						
D			5	1	0	0	4	5	1						
E		5	2	0	0	0	10	3	2						
F		8	1	1	0	0	4	5	5						
8460															
G					1	3	1	0	0	4	10	4	3		
H					6	3	1	0	0	6	3	3	5	1	
I						9	5	0	1	0	2	8	6	0	1

^aD = days from planting to first flower

⁺A = plant row from of a late-generation row

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BIOGRAPHICAL SKETCH

Janvier Emmanuel Bidja Mankono was born on January 1st, 1951, in Abong-Mbang, Cameroon. He completed his secondary education in June 1972. In September 1972, he entered the University of Yaounde where he graduated, in 1977, with a diploma in general sciences with emphasis in agriculture. In October 1977, he was admitted to the National Advanced School of Agriculture (ENSA) where he graduated, in 1977, with the Engineer of Agronomy diploma (with high honors).

After graduation, he joined the ENSA faculty as Assistant Lecturer in the Department of Agriculture. In 1979, Bidja Mankono was admitted to the University of Arizona where he obtained a Master of Science degree in horticulture in 1982. He entered the University of Florida in January 1985. He is currently a candidate for the degree of Doctor of Philosophy, Department of Agronomy, University of Florida.

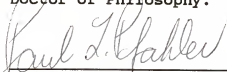
Bidja Mankono is married to Rachel Bidja and has one daughter, Marcelline Armelle Mfegue.

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August 1988



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